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Fitness of experimental populations of *Drosophila melanogaster*

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Document Version

Publisher's PDF, also known as Version of record

Publication date:

1968

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

van Delden, W. (1968). *Fitness of experimental populations of *Drosophila melanogaster**. s.n.

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I. INTRODUCTION

A large discrepancy exists between the potential number of descendants produced by any species and the relatively small number of this progeny which survives and comes to reproduction. The observation that a great part of the new generation is eliminated before its reproductive period formed the starting point for DARWIN'S theory of natural selection. This elimination is brought about by such causes as predation, competition, restricted space, restricted amounts of food, climatic influences etc. Within a population there is, however, variation in the ability to survive. Well adapted individuals have a greater chance of surviving than less well adapted ones: "the survival of the fittest" as DARWIN expressed it in a term adopted from SPENCER. The elimination is accordingly selective: individuals badly fitted to the prevailing environmental conditions are most readily eliminated. Although the term "survival of the fittest" emphasizes elimination, already DARWIN recognized that differential reproduction was an essential part of the fitness concept. Fitness is then defined as the relative ability of individuals to survive and reproduce. When differences in fitness are related to differences in genotype, relative fitness values can be attached to genotypes themselves. Genotypes with a higher fitness pass on their genes more often to the next generation than genotypes with a lower fitness. Many terms are used in the literature for this individual fitness: adaptive value, selective value, reproductive rate, Darwinian or short-term fitness etc. Fitness so defined is a relative intrapopulation measure which provides a means of comparing the various genotypes present in a population. For this purpose a scale running from 0 (no descendants produced) to 1 (the most descendants produced) is often used. In this definition survival is merely one of the aspects of fitness, together with length of reproductive period, fertility, fecundity, developmental rate and many others.

Fitness values must always be accompanied by a description of the environment in which the determination was carried out, fitness being strongly dependent on environmental factors. Fitness relationships between genotypes found in a given environment may be completely different or even reversed in others. Both abiotic and biotic environmental factors are important in this respect. KALMUS (1945) for example found that homozygotes for the *Drosophila melanogaster* mutant *ebony* normally possessed lower fitness than wildtype homozygotes. Low temperature combined with dryness however reversed the fitness relation between these genotypes. The dependence of the fitness of a given genotype on the presence of other genotypes in the same population is well illustrated by some of the extensive experiments of DOBZHANSKY and co-workers on the third chromosome inversion polymorphism in *Drosophila pseudoobscura* (reviews DOBZHANSKY 1951, 1957). Experiments in which three karyotypes at a time were present

(WRIGHT and DOBZHANSKY 1946; LEVENE, PAVLOVSKY and DOBZHANSKY 1954, 1958) made it clear that the fitness ratio of two homo-karyotypes, found when only two karyotypes were present, could be completely reversed by the addition of a third karyotype to the population. These experiments suggested that the fitness of a genotype may also depend from its frequency in the population. Evidence for frequency dependent fitness values has also been brought forward by BAKKER (1961) and KOJIMA and YARBROUGH (1967). It is clear that the fitness of a genotype is not a constant but may change when abiotic or biotic components of the environment alter or when the genetic composition of the population to which it belongs changes.

The average fitness of a population (\bar{W}) can be derived from the fitness of the genotypes present in that population. In the simple case of two alleles A_1A_2 in a randomly mating population with frequencies p and q respectively, where W_{11} , W_{12} , and W_{22} are the relative fitnesses of the genotypes A_1A_1 , A_1A_2 , A_2A_2 whose relative frequencies (f) in the population are p^2 , $2pq$ and q^2 respectively, the average fitness of the population is: $\bar{W} = \sum fW = p^2W_{11} + 2pqW_{12} + q^2W_{22}$ (on the assumption that the fitnesses are independent of the frequencies). As the frequency of the genotypes with low-fitness in the next generation will be decreased by natural selection, the average fitness \bar{W} will increase. It has been shown by WRIGHT (1949) and LI (1955a, 1955b) that a stable equilibrium value of gene frequency yields a maximum value of the average fitness of the population; an unstable equilibrium on the contrary yields a minimum average fitness.

At the population level we are confronted with properties not applicable to individuals such as population size, breeding system, genetic structure etc. It may be asked what interpopulation differences in these characteristics mean for the survival of the populations involved. When we want to compare populations in this respect it is necessary to have a measure of population fitness indicating the relative "success" of the populations. It should be stressed that individual fitness is of little help in this respect for it is defined as an intrapopulation measure. In contrast to genotypes, populations of the same species lose their identity when mixed. It will be clear that the average fitness (\bar{W}) of a population, though useful within a population as an indication of the fitness level reached, is of no use in this context, since this measure is defined with respect to an intrapopulation standard (the genotype with the highest fitness) and cannot be applied to the comparison of populations, having different standards (CAIN and SHEPPARD 1954, 1956; LI 1955b; FISHER 1958).

Though a rigorous definition of population fitness, unlike individual fitness, has not yet been given, a number of experiments in which the relative fitness of populations is compared, have been carried out. What is meant by relative population fitness in these experiments, always has something to do with the "success" of the populations in surviving and leaving offspring but what is actually measured differs from investigation to investigation. In

some experiments (WALLACE 1948, 1952; BUZZATI-TRAVERSO 1955) the estimates of population fitness are mainly based on measurements of components of fitness such as sterility, fecundity, fertility, developmental rate, longevity etc. The drawbacks of this method are obvious: a) fitness comprises many components, not all of which will be measured in the experiment, b) the importance of each component may be unclear, different fitness components may give quite different fitness estimates, c) measurements are generally done on isolated flies under conditions not prevailing in the population and the fitness found may be quite different from that under population conditions.

In a number of experiments WALLACE (WALLACE 1951, 1952, 1956; WALLACE and KING 1951, 1952) tried to measure fitness of *Drosophila melanogaster* populations with the aid of the CyL/Pm technique. The viability of individual second chromosomes in the homozygous state relative to the viability of heterozygotes for that chromosome and the CyL chromosome was determined. The disadvantages of determinations of this type are clear: only part of the entire genome is included and the flies have to be crossed with an unrelated marker strain.

The competitive ability of the population may also be used as a measure of fitness. KNIGHT and ROBERTSON (1957) determined the competitive success of some wild *Drosophila melanogaster* populations by combining flies from these populations and flies from a standard Cy/Pm *Drosophila melanogaster* strain under conditions of severe larval competition. The ratio of emerged wild-type flies to Cy/Pm flies was called the "competitive index" to indicate that what was measured was not completely synonymous with population fitness. BARKER (BARKER 1963a, 1963b, 1965, 1967a, 1967b; CLARINGBOLD and BARKER 1961) used success in interspecific competition as an estimate of relative population fitness. Populations of *Drosophila melanogaster* and *Drosophila pseudoobscura* were each placed in competition with flies from a *Drosophila simulans* strain, the relative fitnesses were then estimated from the rate of change in the frequencies of the two competing species. STRICKBERGER (1963b) also used success in competition as a fitness measure.

The thought underlying many of these and similar experiments is that a population which better exploits a standard environment than another population by producing a greater amount of progeny or biomass, also possesses a higher fitness. (CARSON 1957, 1958a, 1958b, 1961a, 1961b, 1964; BEARDMORE, DOBZHANSKY and PAVLOVSKY 1960; BATTAGLIA and SMITH 1961; DOBZHANSKY and PAVLOVSKY 1961; CANNON 1963a, 1963b; STRICKBERGER 1963a, 1963b; AYALA 1965a, 1965; BATTAGLIA 1965; CRENSHAW 1965).

WALLACE (1959) states that when productivity measurements are made on individual females of a population with regard to an external standard, population fitness equals the average of the individual fitnesses.

The "innate capacity of increase" is also used as an estimate of population fitness (BIRCH, DOBZHANSKY, ELLIOTT and LEWONTIN

1963; DOBZHANSKY, LEWONTIN and PAVLOVSKY 1964; OHBA 1967). This measure implies population growth under "ideal" conditions, i.e. without competition and under optimal abiotic environmental conditions. On the other hand it has also been stated that numerical stability more than rate of increase or absolute population size will be an indication of population fitness (see WILLIAMS 1966 for a review). McDONALD and DAVIDSON (1965) found that a wild strain had a more stable population size than a mutant strain, the latter was much more easily brought to extinction.

I will stress again that each fitness value found, both for individuals and populations, holds only for the environment in which the determination was done. The fitness of a population determined at different times may give quite different results owing to environmental changes or changes in genetic composition of the population. Such "instantaneous" fitness values have consequently only a restricted value. All the measures of population fitness mentioned above are only an indication of the level of adaptation i.e. exploitation of the present environment, at the present time. From an evolutionary viewpoint however it is much more important to know the future "success" of a present-day population, so to have a prognosis of fitness over a long period of time. I will make a clear distinction between this fitness concept of future survival in future environments and the (short-term) fitness of individuals and populations discussed before by calling the former type of fitness: *long-term fitness*.

An important contribution to the concept of long-term fitness is given by THODAY (1953, 1958a). In his view long-term fitness has to be defined in relation to a contemporary group of individuals which will have common descendants in future (a "unit of evolution"). He defines long-term fitness as: "the probability that such a unit of evolution will survive for a given long period of time, such as 10^8 years, that is to say will leave descendants after the lapse of that time". This long-term fitness depends upon a number of components: 1) adaptation, 2) genetic stability, 3) variability (consisting of genetic flexibility and phenotypic flexibility) and 4) stability of the environment. In a constant environment most surviving organisms will be well adapted, there will be selection for genetic stability. But when the environment varies, the unit of evolution must be able to cope with these changes. In general a slight change may be faced with phenotypic flexibility, but a greater change will need genetic flexibility. So there is an antagonism between genetic stability and genetic flexibility, an antagonism which however is weakened by the development of genetic systems which permit cryptic genetic variability (diploidy, dominance, polygenic complexes). The survival of a unit of evolution depends greatly, of course, of the amount of change in environment. THODAY comes to the conclusion that the (long-term) fitness of a unit of evolution increases: "a) by resolution of the antagonism between genetic stability and genetic flexibility b) by increase of phenotypic flexibility c) by adaptation to a stable environment". The difficulty of THODAY'S long-

term fitness concept is the impossibility of measuring it.

LEWONTIN (1957, 1961) proposed an all-or-none fitness concept: if a population can survive and reproduce in more environments than another population, the former possesses a greater fitness. It can then be argued that a population which survives in a greater number of environments than others also has a greater chance to survive future environments. This makes an experimental attack on long-term fitness possible by testing populations in a great number of different environments.

Some fundamental questions connected with the study of population fitness resulting from the preceding pages are:

- a) the search for reliable measures of short-term population fitness,
- b) the measurement of long-term population fitness,
- c) the relation between short-term and long-term fitness,
- d) the relation between the genetic structure of a population and both aspects of population fitness.

The aim of the present study is to provide evidence bearing on these points. Population fitness is here, by analogy with the fitness of genotypes, defined as *relative* success of populations in surviving and reproducing. In order to facilitate research into these four points all populations used in these experiments originated from a *Drosophila melanogaster* strain, inbred for some hundreds of generations. Such a highly homozygous line possesses a low fitness compared with outbreeding lines. When flies of such a strain are put into population cages, mutation will provide genetic variability in the original homozygous strains. Most, if not all, newly introduced alleles will influence the fitness of their carriers. By the working of natural selection those genes, or those combinations of genes at different loci brought about by recombination, giving a higher fitness than others, will increase in frequency. Consequently a rise in population fitness will occur in the course of time. Such adapting populations provide an unique opportunity to study population fitness, for fitness changes in these populations will be unambiguously progressive when a longer period is considered. By measuring, over a long period, a number of classical components of fitness (termed "direct fitness characters"), some characters less obviously connected with fitness ("indirect fitness characters") and the parameters of population size and productivity ("population fitness characters") it was hoped that information relevant to the first three points stated above would be obtained.

Progress in connection with the fourth point would, ideally, call for comprehensive investigation of the architecture of the evolving gene pools. An investigation of this type would represent, in itself, such a large research project that for practical reasons it was necessary to restrict this aspect of the work to multiple assays of the levels of genetic variability in the adapting populations. Two environments were chosen in which to keep the adapting populations, one of these having a constant temperature and one a regularly fluctuating temperature, but with an average

temperature equal to the former. This choice of environments was suggested by observations (BEARDMORE 1961; BEARDMORE and LEVINE 1963) that populations adapted to such a fluctuating environment possess greater fitness and a higher genetic variance than populations from the same origin but kept at a constant temperature.

IX. SUMMARY

1. The present study attempts to examine some aspects of the fitness of populations, here defined as the *relative* success of populations in surviving and reproducing. A distinction was made between short-term and long-term fitness. The aim of the study was to provide some elucidation of the following basic points in the context of population fitness:
 - a. the measurement of short-term fitness.
 - b. the measurement of long-term fitness.
 - c. the relation between short- and long-term fitness.
 - d. the relation between the genetic structure of populations and both types of population fitness.
2. A number of experimental populations of *Drosophila melanogaster* were started from a highly homozygous inbred line. Some populations were kept at 25°C (K), others at a daily fluctuating temperature (V). K and V populations were studied for a period of two years following initiation ("the experimental period"). Another population (α), derived two years earlier from the same inbred line, was also studied. During the experimental period a number of characters were examined at intervals in all populations.
3. The K and V populations showed a considerable and significant improvement in a number of "direct fitness characters" (female fertility, fecundity, egg hatchability, larva-adult survival, longevity and developmental speed). Population α showed an increase in fecundity, longevity and developmental speed.
4. Significant changes were also observed in a number of characters less obviously connected with fitness ("indirect fitness characters"). Of these, sex ratio, body weight, sternopleural chaetae number and asymmetry of the sternopleural chaetae decreased.
5. A pronounced increase in the "population fitness characters" of productivity and population size took place in the K and V populations. Population α also increased in productivity. The coefficient of variation of productivity (and also of a number of direct fitness characters) decreased significantly in the course of the experimental period.
6. The performance in a range of "new" environments, taken as a measure of long-term fitness, increased.
7. Genetic variance, estimated from heritability tests for sternopleural chaetae number, increased.

8. It is concluded that the combined action of outbreeding, mutation, recombination and natural selection was highly effective in bringing about progressive changes in population fitness in the experimental period. The observed divergence of the populations in genetic variance and population fitness is discussed. No systematic differences in genetic variance and fitness were found between the K and V type populations as groups.
9. When populations were ranked for the various direct, indirect and population fitness characters a good concordance was found. It is concluded that productivity and population size provide in general good estimates of population fitness as do fertility, fecundity, asymmetry and coefficients of variation of fitness characters. There is good concordance between the performance in various new environments (except for productivity on a reduced amount of food) and between this aspect of long-term fitness and many of the short-term fitness characters.
Short- and long-term fitness as determined here are strongly positively correlated.
Genetic variability, the only aspect of the genetic structure of the populations considered in the present study, was found to be positively correlated with population fitness.
10. It is argued that estimates of short-term fitness based on only one character have a restricted value. A more general fitness measure based on relative performance in a number of environments and on a combination of criteria is advocated. This should permit quantitative comparisons of the relative fitness of populations and, by allowing predictions of relative future success, has the virtue of being testable.

SAMENVATTING

1. Het onderhavige onderzoek heeft betrekking op enkele aspecten van populatie "fitness", gedefinieerd als het *relatieve* succes van populaties om te overleven en zich voort te planten. Er werd onderscheid gemaakt tussen populatie fitness op korte en op lange termijn. Het onderzoek werd opgezet om informatie te verkrijgen over de volgende fundamentele aspecten van populatie fitness:
 - a. het bepalen van populatie fitness op korte termijn.
 - b. het bepalen van populatie fitness op lange termijn.
 - c. de betrekking tussen fitness op korte en op lange termijn.
 - d. de betrekking tussen de genetische structuur van populaties en beide typen populatie fitness.
2. Uit een homozygote, ingeteelde lijn van *Drosophila melanogaster* werden een aantal populaties aangezet. Sommige populaties werden bij 25° (K) gehouden, andere populaties bij een temperatuur die een dagelijkse fluctuatie onderging (V). Na het aanzetten uit de ingeteelde lijn werden de K en V populaties gedurende een periode van twee jaar ("de experimentele periode") onderzocht op een aantal eigenschappen; dit was ook het geval voor een populatie (α), die twee jaar eerder uit dezelfde ingeteelde lijn was aangezet.
3. De K en V populaties toonden in de loop van de experimentele periode een aanzienlijke verbetering in een aantal, direct met fitness verbonden eigenschappen als fertiliteit, eiproductie, uitkomen van eieren, overleving van larve tot adult, levensduur en ontwikkelingssnelheid. Populatie α toonde een toename in eiproductie, levensduur en ontwikkelingssnelheid.
4. Ook werden veranderingen geconstateerd in eigenschappen die niet als directe fitness eigenschappen te beschouwen zijn ("indirecte fitness eigenschappen"). Aangetoond werd dat sex ratio, lichaamsgewicht, sternopleuraal chaetae aantallen en asymmetrie afnamen.
5. Een sterke toename in produktiviteit en populatiegrootte werd vastgesteld in de K en V populaties, verder toonde populatie α een toename in produktiviteit. De coëfficiënt van variatie van produktiviteit (en ook van een aantal directe fitness eigenschappen) gaf een daling te zien in de loop van de experimentele periode.
6. Produktiviteit en larve-adult overleving in "nieuwe" milieus, gebruikt als maat voor fitness op lange termijn, namen toe gedurende de experimentele periode.

7. Genetische variantie, bepaald uit de erfelijkheidsgraad voor sternopleurale chaetae, nam toe.
8. Geconcludeerd wordt dat in de populaties door de gezamenlijke werking van mutatie, recombinatie en natuurlijke selectie in de loop van de experimentele periode aanzienlijke, progressieve, veranderingen in populatie fitness tot stand zijn gebracht. De waargenomen divergentie van de populaties in genetische variantie en populatie fitness werd besproken. Tussen de K en V populaties als groepen werden geen systematische verschillen in genetische variantie en fitness aangetoond.
9. Fitness-rangordes volgens de verschillende directe, indirecte en populatie fitness eigenschappen stemden in hoge mate overeen. Geconcludeerd wordt dat produktiviteit en populatiegrootte, evenals fertiliteit, asymmetrie en de coëfficiënt van variatie van fitness eigenschappen in het algemeen een goede schatting van populatie fitness gaven. Fitness-rangordes voor de verschillende nieuwe milieus toonden een grote mate van overeenstemming (een uitzondering vormde reductie van de voedsel hoeveelheid). Er bestond een positieve correlatie tussen fitness op lange en op korte termijn. Genetische variabiliteit, het enige aspect van de genetische structuur van de populaties dat in dit onderzoek werd onderzocht, bleek positief gecorreleerd te zijn met populatie fitness.
10. Daar schattingen van fitness op korte termijn, gebaseerd op één eigenschap, slechts een beperkte waarde bezitten, wordt een meer algemene fitness maat voorgesteld. Een dergelijke fitness maat zou gebaseerd moeten zijn op een combinatie van criteria en zou bepalingen in verschillende milieus moeten omvatten.